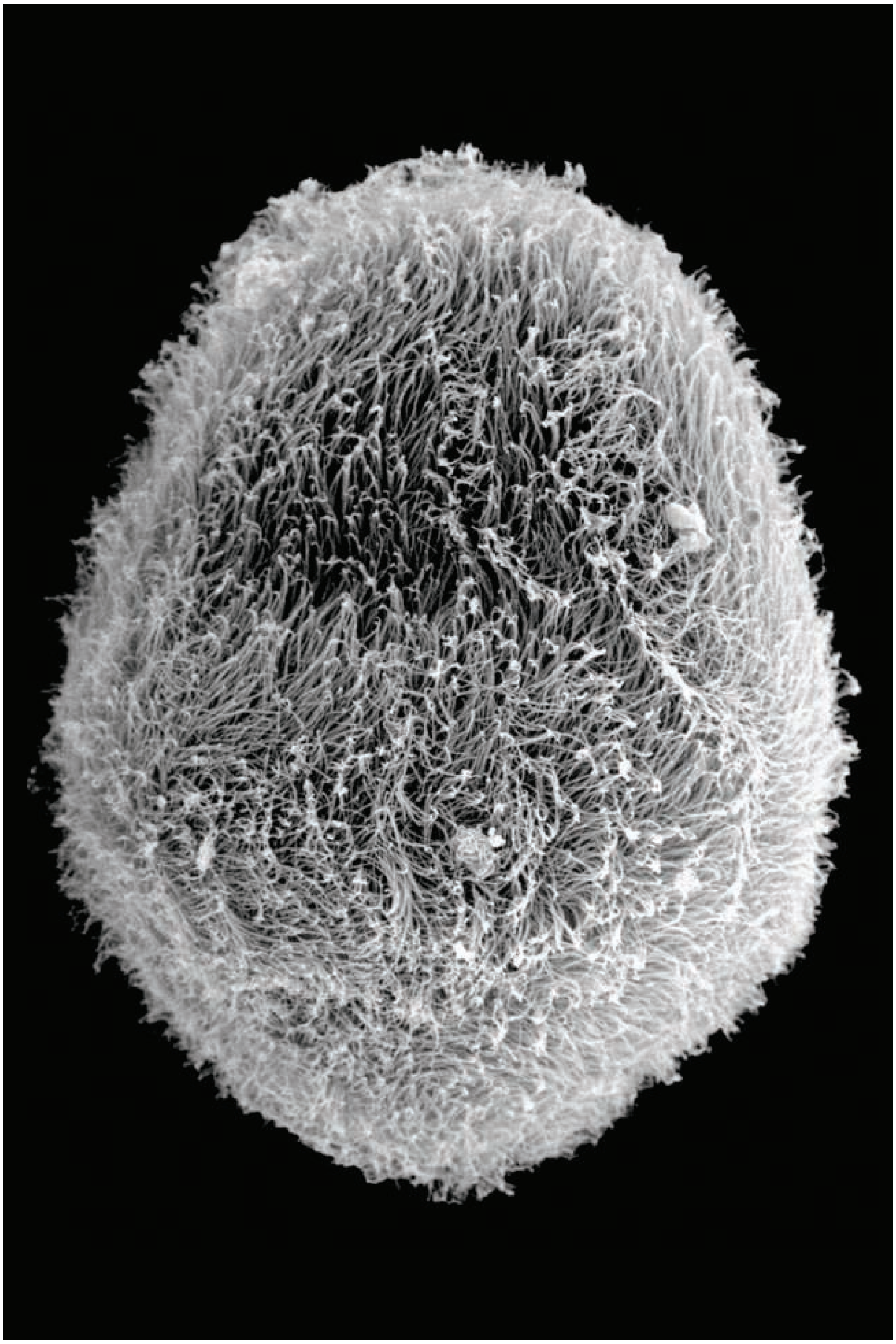
The mother of us all

We may be the descendants of a sponge larva that refused to settle down, reports Bob Holmes



DR. ALEXANDER ERESKOVSKY

CALL it CSI: Precambrian. About 700 million years ago, one of the most significant – and most mysterious – events in the history of life on Earth occurred. Suddenly, there was more to life than just single-celled microbes. Within a few tens of millions of years, an extraordinary array of large animals appeared, armed with jaws and claws and eyes and brains.

Yet we still know surprisingly little about the origin of multicellular animals. "The different branches of the animal tree evolved very rapidly in a short period, a long time ago," says Nicole King, an evolutionary biologist at the University of California, Berkeley.

The very first animals left few fossil traces. What they did leave were lots of descendants. It is to these descendants that evolutionary detectives have to turn to reconstruct the events of those early years. By comparing the genes of living organisms and painstakingly working out their family trees, they are slowly building up circumstantial evidence and piecing together a sketch of that first animal, our great-to-the-*n*th-grandmother. And not

Free-swimming sponge larvae (left) are nothing like the adults (below)

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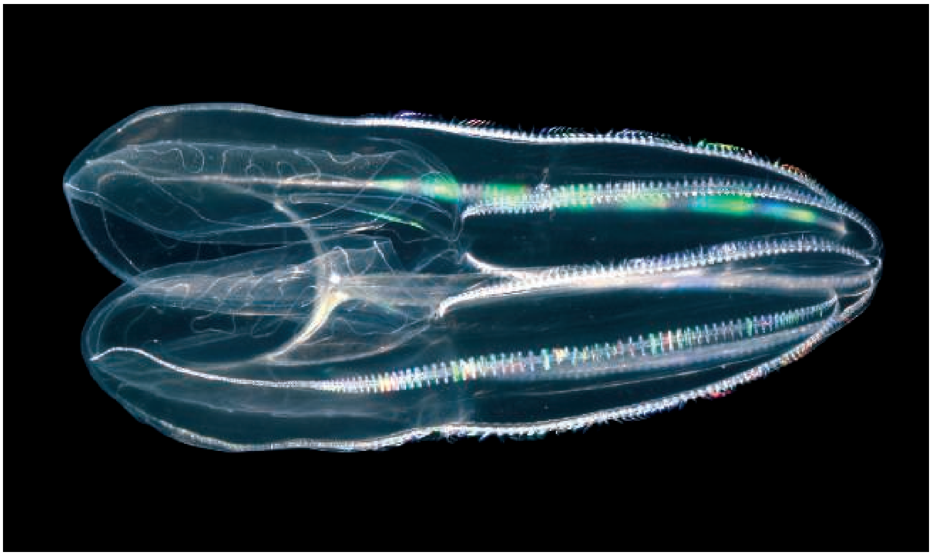
Comb jellies and hydras branched off early in animal evolution



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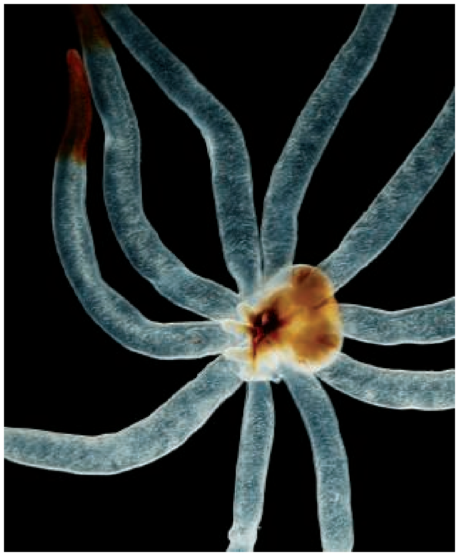

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just its appearance – the detectives are also coming up with a motive, a reason why animals evolved when they did.

The closest living relatives of multicellular animals, or metazoans, have long been considered to be an obscure group of single-celled creatures called choanoflagellates. These little microbes filter food from water using a tail, or flagellum, set in the middle of a crown-like collar. The feeding cells of sponges bear a similar collar – a hint that the earliest metazoan might have been sponge-like. More recently, DNA sequence comparisons have confirmed this close kinship.

However, sponges seem unlikely ancestors. They are little more than a loose assemblage of cells that lack the true tissues and organs found in higher animals. Plus their structure – a porous mass of interconnected water channels – is nothing like that of any other animal. As a result, most zoologists tend to put sponges on a side branch of the animal tree, an abortive experiment that led nowhere. That's what makes Kevin Peterson's results so thought-provoking.

Peterson, a molecular palaeobiologist at Dartmouth College in Hanover, New Hampshire, and his colleagues compared the sequences of seven genes from 42 species of animal, and then used sophisticated computer programs to assemble the species into the most likely evolutionary tree. Sure enough, sponges branch out near the base – but Peterson's tree differs from most others in a subtle but hugely significant way. Instead of putting sponges on a single side branch, Peterson's tree has sponges on both sides of the trunk.

"Our great-to-the-*n*th-grandmother was a hungry sponge larva. Put that on your family tree"

In other words, the ancestor of all complex animals not only resembled a sponge, it actually was a sponge. "If you had a time machine and brought back the last common ancestor of all living animals, and you gave it to an invertebrate zoology class, they'd call it a bath sponge," says Peterson.

Peterson's conclusion is highly controversial. Other research teams, using similar analyses but an alternative selection of species and different DNA sequences, have fingered other animal groups as most resembling the ancestor.

For example, a study based on DNA sequences and morphological characteristics of 24 metazoans suggests that the ancestral metazoan most likely resembled not a sponge but an obscure modern-day animal called a placozoan (*PLoS Biology*, vol 7, e20).

Placozoans are little more than sheets of cells a few millimetres long, with no gut, nerves or muscles. Despite this, they can swim and crawl. Their simplicity makes them a likely model for the common ancestor – except that there might be more to placozoans than we know. Their sex lives are a mystery, for instance, even though DNA analyses show they must have sex.

Another study, of 150 genes in 77 species, puts yet another animal group, the jellyfish-like ctenophores, at the base of the metazoa (*Nature*, vol 452, p 745). Others scoff at this possibility, since ctenophores are relatively sophisticated predators, which seem unlikely to have evolved before there were other large organisms to prey on.

Just last month, a new animal tree based on 128 genes from a wide range of animals put sponges as a separate group, distinct from the lineage leading to › higher animals (*Current Biology*, DOI: 10.1016/j.cub.2009.02.052). If this is right, the ancestral metazoan might not have been spongelike in form. Peterson, however, says his latest analysis – as yet unpublished – shows this tree is incorrect.

Perhaps all one can conclude from these attempts to sort out the base of the animal tree is that it is still early days. "So far, the data sets we have do not show robustness. When you add new species, you find different things," says evolution biologist Antonis Rokas of Vanderbilt University in Nashville, Tennessee. "That makes me think it is more wobbly than these authors would have us believe."

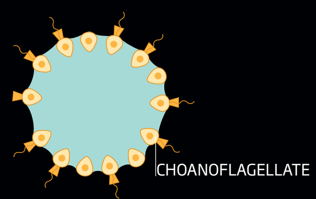
On balance, though, most experts think Peterson is probably on the right track. "I think the weight of evidence favours the notion that sponges evolved first," says King. "These other observations are interesting, and we can't rule out the possibility that they might gain more support, but right now the majority of the field is comfortable with the notion that sponges are the earliest-branching."

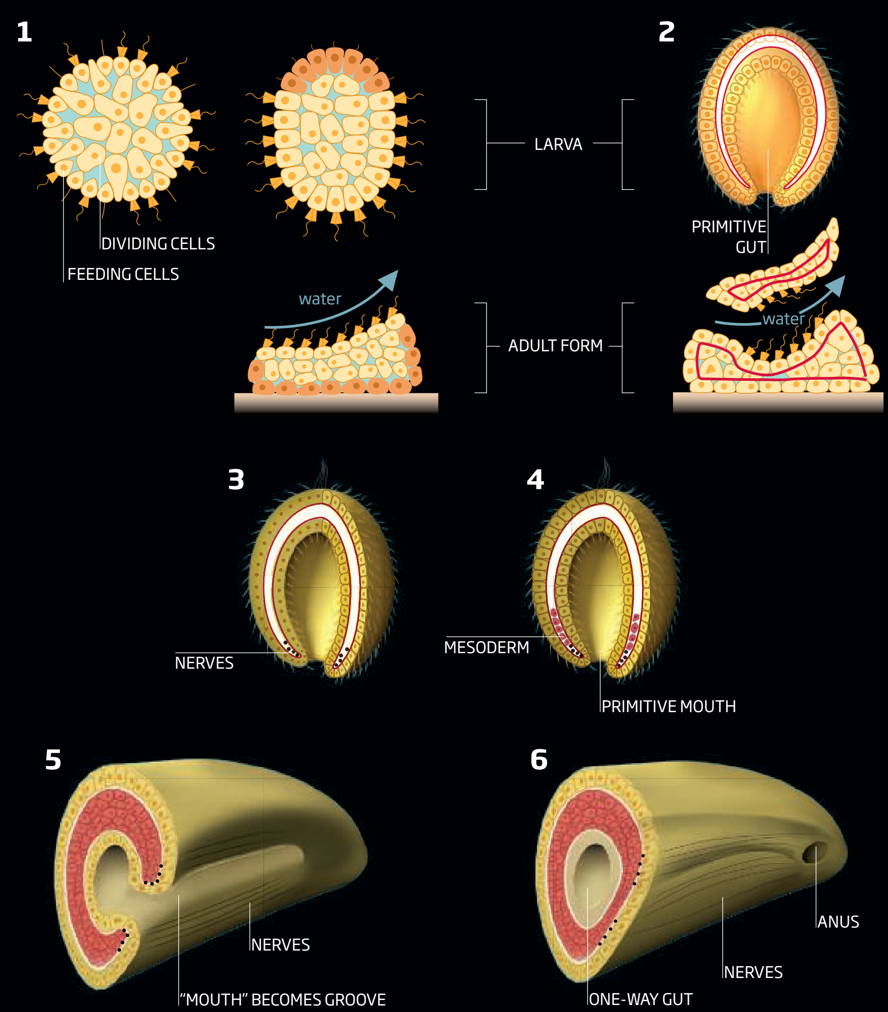
So how does that square with the bizarre anatomy of sponges, which would seem to rule them out as the ancestor of higher animals? It is difficult to envision a stepwise progression from adult sponges to more complex animals – but it probably did not happen that way, says Claus Nielsen, an evolutionary morphologist at the University of Copenhagen in Denmark.

Sponges produce free-swimming larval forms not unlike some conceptions of the ancestral animal. These larvae typically live off stored nutrients and settle on the sea floor after a few days. The larvae of one early sponge, however, might have evolved ways

Six steps from single cells to complex animals

Claus Nielsen of the University of Copenhagen, Denmark, has proposed that multicellular animals evolved from single-celled organisms in six major steps. Here is a simplified version of his proposed steps. The details of early animal evolution are still hotly debated, however, and his scenario is just one of many competing ones





STARTING POINT CHOANOFLAGELLATES

Single-celled filter feeders called choanoflagellates are the closest relatives to multicellular animals. Some form colonies, but all the cells are situated on the outside surface and there is no division of labour.

STEP 1 MULTICELLULARITY EVOLVED

The individual cells started to stick together more closely. At least a few of the specialised molecules that multicellular animals use for this job, called cadherins, have been found in the genome of solitary choanoflagellates by Nicole King of the University of California, Berkeley. King speculates that choanoflagellates might use cadherins to detect and identify bacterial prey species. Later, these molecules were co-opted for use in holding cells together.

Other molecules made transport between the cells possible, allowing food to be shared. This meant cells on the outside could feed while those in the centre were dividing, for instance. Since single cells have to stop feeding in order to divide, this division of labour allows faster growth.

As the early multicellular organisms grew

STEVE GSCHMEISSNER/SPL

Even worms have all the key features of complex animals

of feeding during the larval stage and could thus have remained free-swimming for far longer than normal. Eventually these "larvae" might have begun breeding too, abandoning the "adult" bottom-dwelling stage altogether.

In this scenario, most of the anatomical problems disappear, Nielsen says. He has set out in detail (see below) how sponge larvae may have evolved into higher animals (*Evolution and Development*, vol 10, p 241).

All the intermediate organisms in the progression make sense as living, feeding animals – something that is not necessarily true of other, competing scenarios, Nielsen says. "The problem with older theories that started with a ball of cells is that nobody has speculated on how this organism could feed."

A scenario like Nielsen's would help make sense of the sudden burst of animal forms that appears in the fossil record, says Peterson. A world filled solely with soft-bodied sponges filtering bacteria and organic debris from the seawater would leave few fossils and show little morphological change. "Sponges would be palaeontologically invisible," he says. What's more, with nothing but sponges around, there would have been little selection pressure to drive further evolution. "There are no predators in the world's biota. There are no arms races. Effectively, there's no macroevolution."

Then, about 700 million years ago, the Earth's oceans froze over, or nearly so, at least once. During this "Snowball Earth" phase, there would have been fewer and fewer suitable spots for sponge larvae to settle on, says Peterson. Larvae that could drift with the currents for longer would have had a better chance of finding a suitable spot – and any larvae that could take in food while they drifted would thus have had a huge advantage.

Eventually, Peterson speculates, some evolved a rudimentary gut. "Most of the genes are there. The ability to digest is there. You just need to get that opening," he says.

With the help of crude guts, some of these early animals may have started to feed on others. This emergence of multicellular animals that preyed on other multicellular animals – however primitive – would have changed everything. Predators capable of chasing and overpowering their prey would have a huge advantage. Potential prey would have to detect and evade the predators to avoid becoming another meal.

The result is an arms race, says Peterson. "You just get better and better with muscles and nervous systems and sense organs." That would have set the stage for the explosive diversification of animal forms that we see in the fossil record.

"You've got these two remarkable singularities – Snowball Earth and the origin of complex animals – at the same time. Is it just a coincidence? I don't think so," says Peterson. If he's right, and if Nielsen's scenario for animal evolution is accurate, then that shadowy being in the oh-so-distant past, our great-to-the-*n*th-grandmother, was a hungry sponge larva. Put that on your family tree. ■

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larger, some started to settle on the bottom, developing folds and internal passages to increase the surface area for feeding. The result was a sponge, but the larval stage remained free-swimming, and later became supplied with yolk, so it did not need to feed.

STEP 2
EXTRACELLULAR DIGESTION AND SEALED EPITHELIA EVOLVED

Sponges feed on small particles that individual cells capture and digest intracellularly, which limits the size of food particles. At some point, a sponge larva acquired the ability to consume larger food items by developing a watertight layer of cells, or epithelium. This meant digestive enzymes could be secreted into an enclosed space formed by the epithelium – a primitive gut – without being lost to the surroundings through diffusion.

Once larvae could feed themselves, the larval stage became ever more extended. Some started reproducing and eventually the "adult" sponge stage was lost altogether.

Nielsen envisions extracellular digestion evolving in a sponge larvae, but a similar state of organisation can be seen today in placozoans. These consist of little more than a flat sheet of cells with a digestive epithelium on the underside, which can be pressed against a food item.

STEP 3
NERVOUS SYSTEM EVOLVED

For animals to respond to the environment, their cells have to talk to each other. The nervous system began to evolve when some cells started to specialise in sensing changes in the environment – such as when a larva has settled on a surface – and communicating this with other cells by releasing specific chemicals. Animals feeding on larger food items would have benefited greatly.

Bernard Degnan's team at the University of Queensland in Brisbane, Australia, has found many of the genes now involved in communication between nerve cells are present in the genome of sponges. While sponges have no nervous system, they do have basic sensory abilities, with some larvae able to swim away from light, for instance.

STEP 4
MESODERM EVOLVED

The middle tissue layer, or mesoderm, gives rise to many of the key internal organs of animals, including muscles, the circulatory system, and the excretory system. The evolution of this tissue layer – found in all animals more complex than jellyfish and hydras – would have provided a huge boost to the abilities of both predators and prey. Circulatory and excretory systems made possible the evolution of much larger organisms, which no longer had to depend on diffusion to get oxygen and eliminate waste.

STEP 5
BILATERAL SYMMETRY EVOLVED

Early animals were either asymmetrical blobs, such as sponges, or radially symmetrical organisms, such as jellyfish. As animals became more sophisticated and mobile, their shape became more worm-like and the sense organs became concentrated at one end, the head. The result was bilateral symmetry, a feature seen in all higher organisms. (Even starfish and sea urchins, which are radially symmetrical as adults, evolved from bilateral ancestors and are bilaterally symmetrical as larvae.)

Precursors of the genes that define the head-to-tail axis, a group known as *Hox* genes, are present in earlier, non-bilateral forms.

STEP 6
THE ONE-WAY GUT EVOLVED

Jellyfish and flatworms have just one opening to their gut, which means any food waste must leave through the same opening. The evolution of a one-way gut with separate mouth and anus makes digestion more efficient by allowing the gut to specialise, with different parts performing different digestive tasks . In one group of animals, the "old mouth" stretched out, forming a groove. The separate mouth and anus were created when the sides of this groove fused together. (In another major group, the one-way gut may have evolved in a different way.)

With this final step, early animals acquired all the key features found in higher animals.